Kelp forests in False Bay: urchins vs. macroalgae in South Africa's south-west coast biogeographical transition zone.

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Abstract

There is ongoing global concern over unwanted regime shifts in marine systems. Shifts from diverse and productive algal-dominated ecosystems to less productive urchin and coralline-dominated temperate reefs are becoming increasingly common. Kelp forests found along South Africa's south-west coast between Cape Point and Cape Agulhas occur in a region of biogeographical overlap. They are commonly referred to as transition zone kelp forests and are dynamic ecosystems that are particularly susceptible to grazing influence from species such as sea urchins. This study (1) explores the uniformity of these transition zone kelp forests along the western side of False Bay, with a focus on macroalgae and urchins, (2) identifies a threshold in urchin density above which algal abundance declines and (3) seeks to identify relationships between attached and drift algal abundance. Twenty replicate quadrats were sampled in six kelp forests along the western side of False Bay. Within each quadrat, urchins (*Parechinus angulosus*) and kelps (*Ecklonia maxima*) were counted, percentage covers of various understorey algal species were recorded and drift algae were collected. Although there was significant variability in algal and urchin cover across the six sites, kelps generally increased from north to south, while urchins did the opposite. Urchins were negatively correlated with algal communities, and a localised threshold of 1.43kg/m^2 (50 urchins/m^2) was identified, above which attached kelp density failed to increase above 10/m^2 and percentage cover of understorey algae usually remained below 20%. Surprisingly, no relationship was discovered between abundance of drift kelp and attached kelp, understorey algae or urchin density. This result was likely distorted by the naturally turbulent conditions of South African waters. Results highlight the complexity of these cool-water environments. To better understand the role of urchins in this system, experimental research into the feeding behaviour and effect of *P. angulosus* on kelps and understorey seaweeds in the presence/absence of drift algae is advised.

1. Introduction

1.1 Kelp forests in a changing climate

Across the world, kelp forests act as important components of near-shore temperate ecosystems. They provide a source of food and shelter for a variety of organisms and act as nursery grounds for many invertebrate and fish species (Steneck et al. 2002; Steneck & Johnson, 2013). These coastal, cool-water marine environments also provide important ecological and economic services to humans, particularly, the extraction of natural resources and, tourism and recreation (Tegner & Dayton, 2000; Steneck & Johnson, 2013; Bennett et al. 2016; Blamey & Bolton *in press*). Climate change and overexploitation of marine resources, however, are two of the largest challenges facing the structure and function of marine ecosystems, with kelp forests being no exception (e.g. Ling et al. 2009). Kelp forests are influenced by abiotic factors such as temperature, light and turbidity (Dayton, 1985), and their community composition is also mediated by biotic interactions such as predation, herbivory, competition and facilitation (Velimirov et al. 1977; Blamey & Branch, 2012; Steneck & Johnson, 2013). In many parts of the world, ocean warming is already impacting canopy forming seaweeds e.g. Australia (Wernberg et al. 2010, 2011, 2016), Spain (Duarte et al. 2013) and the UK (Smale et al. 2015). Once removed, these kelp canopies are often replaced by either urchin barrens or algal turfs, depending on the site's unique biotic and abiotic conditions. It is likely that kelp forests at low latitudes, which occupy the warmest parts of their range, will be most vulnerable to the ongoing direct and indirect threats of ocean warming, acidification and eutrophication (Scheffer & Carpenter, 2003; Steneck & Johnson, 2013; Provost et al. 2017).

In some regions, kelp forest ecosystems are particularly susceptible to the influence of destructive herbivory, most notably by sea urchins (Scheibling et al. 1999; Tegner & Dayton,

2000; Steneck et al. 2002; Flukes et al. 2012). Phase shifts from supposedly stable kelp forests, to patches of high urchin density, have been recognised in a number of localities (Harrold & Reed, 1985; Scheibling et al 1999; Steneck & Johnson, 2013). These dense patches of urchins are often dominated by extensive encrusting coralline algal communities, but also articulated coralline red algae. However, the loss of canopy-forming algae increases light penetration and can lead to the bleaching – and subsequent dying – of encrusting coralline algae (Irving et al. 2004). In these cases, patches of high urchin density are characterised by a paucity of coralline communities. The two alternating states have been identified as urchin dominance (commonly referred to as "barrens") and kelp dominance (Harrold & Reed, 1985). The former is ultimately considered undesirable as they have negative effects on local biodiversity and fisheries (Ling et al. 2009, 2015). The extent of these shifts varies considerably among geographic locations and most examples have been identified in the northern hemisphere where urchins are often considerably larger than their southern hemisphere counterparts, reach higher abundances and exhibit ferocious, active grazing (Harrold & Reed, 1985; Scheibling et al. 1999; Vanderklift & Kendrick, 2005; Steneck & Johnson, 2013).

The Australian state of Tasmania is an example of one southern hemisphere region that has experienced localised shifts to "urchin dominance". A decline in kelp cover has been indirectly attributed to two drivers, which have intensified consumptive pressures. Firstly, the intensification of the warm, nutrient-poor East Australian Current (EAC), which currently extends ~350km further south than it did in the 1950s, has resulted in the poleward expansion of the urchin *Centrostephanus. rodgersii.* Secondly, the ecological overfishing of large rock lobsters – the main predator of *C. rodgersii* – has drastically reduced the lobster population size structure and abundance (Ling et al. 2009). This has led to reduced predation on *C.*

rodgersii, thereby indirectly intensifying the grazing pressures upon these kelp forests. Temperature changes have, therefore, indirectly impacted kelp forests by altering ranges of habitat-modifying species. In addition, elevated temperatures, such as those now experienced because of the intensification of the EAC, have been found to affect the feeding behaviour of rock lobsters, by reducing their consumption of urchins (Provost et al. 2017). The combined effect of these drivers has led to an increased presence of small urchin dominated (barren) patches within the dense macroalgal beds of Tasmania – a condition referred to as 'incipient' barrens (Johnson et al. 2005, 2011; Ling, 2008).

Furthermore, kelp forests are susceptible to competitive pressures from algal turfs. Mesocosm experiments by Provost et al. (2017) concluded that turf algae responded positively to declining kelp biomass and ocean acidification, supporting findings by Connell & Russell (2010). Connell & Russell's (2010) experimental results in kelp-turf transitions suggested that turf algae can inhibit kelp recruitment, thereby outcompeting them within more acidic, warmer waters. These findings suggest that kelp loss could be exacerbated and their resilience weakened in both kelp-barren and kelp-turf shifts. More frequent and significant phase shifts to systems with reduced trophic levels may, therefore, occur as a result of changing climatic conditions, aggravated by the additional influence of anthropogenic activities, such as overfishing (Jackson et al. 2001; Connell & Russell, 2010).

1.2 South African kelp forest ecosystems and the role of the urchin Parechinus angulosus

In South Africa, four species of kelp exist: *Macrocystis pyrifera* 'angustifolia', *Laminaria pallida, Ecklonia maxima* and *Ecklonia radiata*. Of these, only two species are dominant, *E. maxima* and *L. pallida*. These species form extensive kelp forests that primarily extend from Cape Agulhas in the south to Namibia in the north-west. The region from Cape Point to Cape

Agulhas is recognised as a transitional zone of biogeographical overlap between the Benguela Marine Province and the Agulhas Marine Province (Anderson et al. 2009). Kelp forests found along the west coast – which forms part of the Benguela Marine Province – differ somewhat in their composition to those found along the south-west coast – which forms part of the transition zone. Along the west coast, understorey algal biomass – primarily dominated by *Rhodophyta* at shallow depths of <5m – is greater while grazers are uncommon. In comparison, east of Cape Point, in False Bay (the transition zone), understorey algal biomass – primarily dominated by *Chlorophyta* at shallow depths of <5m – is reduced, while grazers and encrusting corallines are abundant (Anderson et al. 1997; Leliaert et al. 2000). The biomass compositions of understorey algae also differ on either side of the Peninsula, likely as a result of sea temperature, wave exposure, and differing grazer abundance (Leliaert et al. 2000; Tegner & Dayton, 2000). To date, much research has focused on exploring these trophic interactions (see Branch, 2008 for a review), as grazing has been viewed as a major controlling factor for algal species composition (Velimirov et al. 1977; Fricke, 1979; Leliaert et al. 2000).

The dominant grazer in False Bay is the echinoderm, *Parechinus angulosus*; this urchin is numerically abundant in shallow waters of 2-5m (Griffiths, 1981; Anderson et al. 1997) and its abundance has been directly linked to the presence of kelp, given that it feeds almost exclusively on algae, predominantly *E. maxima* (Fricke, 1979, 1980). While some studies have found negative associations between urchin density and algal biomass in the south-west coast transition zone kelp forests (Fricke, 1979; Anderson et al. 1997; Blamey & Branch, 2012), others report no change in algal biomass or kelp recruit densities at sites protected from urchins (Day & Branch, 2002a). This is most likely a result of their feeding behaviour not exerting top-down consumer effects. It has been argued that *P. angulosus* is a debris

feeder rather than a grazer (Velimirov et al. 1977; Field et al. 1980) because it generally feeds on detached algae or drift kelp that has fallen to the sea floor, rather than actively attacking kelp stipes. It is for this reason that *P. angulosus* is thought to have a subtle influence on South African kelp forest composition as, unlike its northern hemisphere counterpart *Strongylocentrotus*, it does not form feeding fronts (Anderson et al. 1997) and it is only during extremely calm conditions that *P. angulosus* has been seen climbing kelp stipes (Fricke, 1979) or grazing on haptera (Anderson et al. 1997).

On the other hand, an urchin exclusion study by Fricke (1979) found that *P. angulosus* does affect the establishment of new kelp plants by actively grazing on young sporophytes, thus limiting kelp recruitment. In some regions, this active grazing may be a result of a switch in feeding mode due to reduced availability of drift algae. For example, *P. angulosus'* northern hemisphere counterpart, S*trongylocentrotus franciscanus*, switches from largely sedentary feeding to active grazing, when there is a decline in drift algae (Harrold & Reed, 1985). However, this kind of behavioural switch, in the absence of drift algae, has not yet been recognised in the locally occurring *P. anugulosus*. If an external disturbance were to deplete an area of South African kelp forest, active grazing on young sporophytes – witnessed by Fricke (1979) – could limit kelp recovery in areas with high urchin density, resulting in coralline-dominated areas (Fricke, 1979; Anderson et al. 1997; Blamey & Branch, 2012). Kelps, however, seem to exert two techniques of self-facilitation to combat these interactions. Firstly, sweeping fronds of *L. pallida* act as a form of protection against herbivory and clear suitable areas for plant colonisation (Velimirov & Griffiths, 1979). Secondly, Anderson et al. (1997) found that in areas of high grazer density (typical of the south-west coast transition zone), a disproportionately high ratio of kelp recruits settle on adult kelp holdfasts, implying that these mature holdfasts act as important refuges for young *E. maxima* sporophytes. These

complex mechanisms of self-facilitation by kelp and the feeding behaviour of *P. angulosus*, may explain why extensive urchin barrens are uncommon in South Africa, compared to the rest of the world (Dayton, 1985), but may also explain why small intermittent patches of urchins can and do exist.

1.3 Significance of the study

There is ongoing global concern over unwanted regime shifts, from algal-dominated ecosystems to urchin-dominated temperate reefs (Ling et al. 2015) as these shifts are often thought to be discontinuous (Filbee-Dexter & Scheibling, 2014). These discontinuous shifts are characterised by hysteresis (i.e. the condition of more than one stable state), which reflects the fact that once an alternative stable state has been reached, its reversal may be difficult to achieve (Scheffer & Carpenter, 2003). For example, if a kelp forest were to recover from an urchin barren state, urchin densities would need to decline to a level much lower than what originally caused the shift (Steneck & Johnson, 2013). The resultant tipping and recovery points mean that there can be a range of densities in which urchins support little or no kelp. It can therefore be difficult to identify a clear threshold in urchin density, above which there is a decline in macroalgae. However, given the ecological and economical importance of kelp forests it is crucial to monitor these systems in an attempt to understand and identify localised tipping points, so that the collapse of such preferred stable states can be prevented (Ling et al. 2015).

Furthermore, transition zone kelp forests are increasingly vulnerable to human-derived stressors, climate change, predation and herbivory, making them one of the most dynamic ecosystems in the world (Steneck & Johnson, 2013; Ling et al. 2015). Extreme weather events, such as droughts, floods, heat waves and storms are anticipated to become more

frequent because of climate change (Kerr, 2011). Worldwide, some regions have already started experiencing the impacts of such extreme climatic conditions; both directly because of rising sea surface temperatures (Wernberg et al. 2013) and indirectly as a result of climate-driven changes in biotic interactions, such as herbivory (Vergés et al. 2014). Along the South African coast, offshore waters have warmed, while coastal waters along the south-west coast are thought to have cooled in recent decades (Rouault et al. 2010, Blamey et al. 2015). *E. maxima* has recently spread 70km east of its original range (Bolton et al. 2012), but has also increased in abundance in transition zone kelp forests (Reimers et al. 2014). Despite this, it is not yet known whether marine systems in South Africa are likely to experience an increase in the frequency and intensity of extreme climatic events such as heat waves and storms.

In South Africa, there is contrasting evidence on the exact role of herbivorous urchins in transition zone kelp forests. Although extensive urchin barrens do not occur in this region, dense patches of urchins are probably able to keep algal biomass to a minimum and limit kelp recruitment. Whether this may change in the future under a changing climate remains unclear. As part of a larger project towards identifying how these systems might change under increased stressors, this study aims to provide a baseline of urchin and algal abundance across a range of sites in False Bay. Firstly, by quantifying the extent of urchin patches and associated algal biomass in False Bay kelp forests, and secondly, by examining correlative relationships between densities of urchins relative to attached kelp, understorey algae, drift kelp and kelp recruits, including the identification of a threshold in urchin density, above which macroalgae is limited. The sites chosen were located on the western side of False Bay because *E. maxima* has shown marked expansion and densifications along this coastline (Reimers et al. 2014). Several sites had also been studied in the past, which allowed for comparison. In this thesis, I addressed the following questions: (1) Are kelp forests along the

western side of False Bay uniform in structure and understorey algal species composition? (2) Can we identify a threshold in urchin density, above which kelp and understorey algal biomass decline? And (3) are quantities of drift algae greater in the presence of attached kelp and understorey algae? Firstly, I hypothesised that kelp forests along the western side of False Bay would not be uniform in structure and algal species composition. This is because kelp forest ecosystems are particularly sensitive to both abiotic and biotic conditions, which are highly unlikely to be identical at separate sites. Secondly, I hypothesised that understorey algae, kelp density and kelp recruits would be negatively correlated with urchin density, because urchins are thought to feed on young kelp sporophytes, thereby limiting kelp recruitment. Thirdly, I hypothesised that drift algae would be positively correlated with understorey algae, kelps and urchins because a site with more algae, would be expected to produce more drift algae through wave action. Urchins are also known to trap drift algae in their spines before feeding, so it is hypothesised that an increased number of urchins would result in an increased quantity of drift kelp trapped within the quadrat.

2. Methodology

2.1 Study sites

Six sites were surveyed along the western side of False Bay in South Africa – a transition zone between the cooler temperate west coast and warmer temperate south coast (Bolton, 1986). From north to south the study sites were: A-Frame [34°12'23.03"S 18°27'33.48"E], Miller's Point New Slipway [34°13'44.13"S 18°28'20.07"E], Miller's Point Old Slipway [34°14'4.95"S 18°28'31.60"E], Partridge Point [34°15'19.61"S 18°28'38.35"E], Bordjiesrif [34°18'46.49"S 18°27'46.70"E] and Buffels Bay [34°19'21.68"S 18°27'50.19"E] (Fig. 1). The two southernmost sites were within the boundaries of Table Mountain National Park.

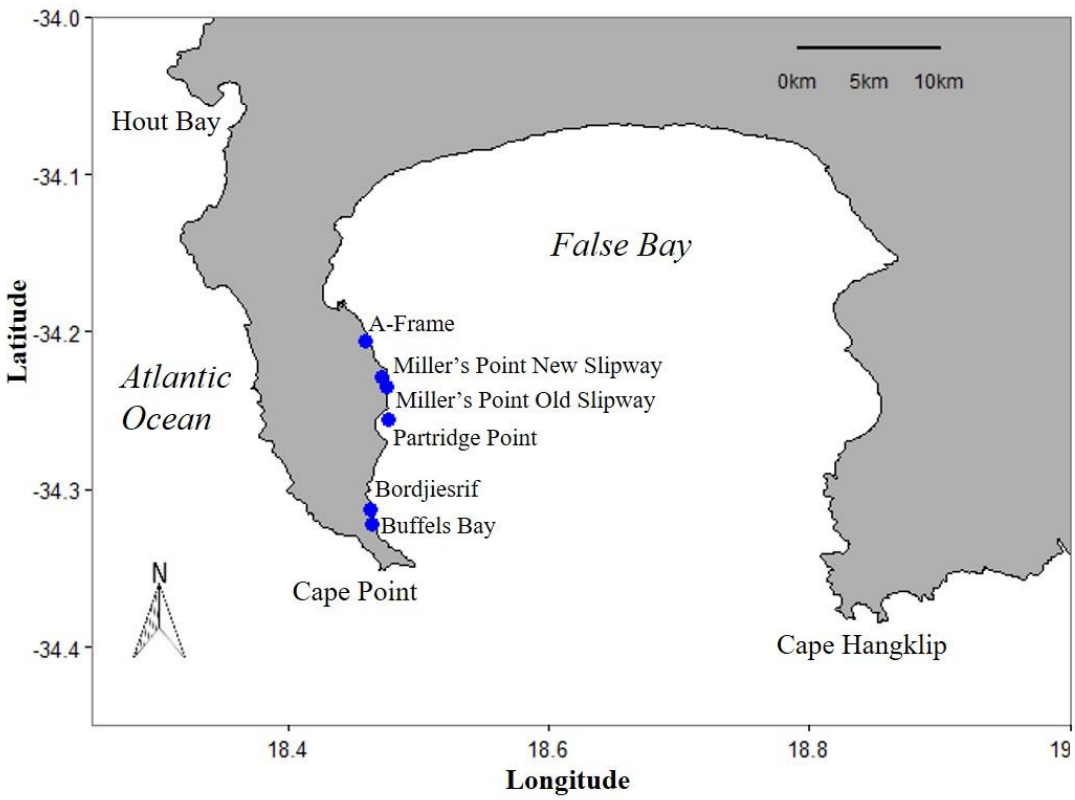


Figure 1: *Location of the six study sites along the western side of False Bay, South Africa.*

Site selection was based on accessibility and those used in previous studies (Fricke, 1979; Anderson et al. 1997; Leliaert et al. 2000; Day & Branch, 2000; Day & Branch 2002a, 2002b). Transition zone kelp forests were visible from the shore for each site, and each site allowed for quadrats to be placed at a depth of between 2 and 5m (Fig. 2).

Figure 2: *Kelp forests visible from the shore at Millers Point Old Slipway (left) and a quadrat at Bordjiesrif (right).*

2.2 Data collection

All data were collected in the month of October (austral spring) 2016 to ensure consistency and reduce inter-seasonal variability, as kelp growth and urchin movement may vary throughout the year depending on seasonal conditions and their reproductive cycles (Fricke, 1979).

At each site 20 x 1m^2 quadrats were surveyed at depths of 2-5m. Anderson et al. (1997) noted that this shallow depth range is where *P. angulosus* is the most abundant grazer in False Bay. By sampling at this specific range, I would reduce biotic differences that may vary with depth. Four 10m long transects were placed randomly at 5m intervals within a kelp forest at each survey site. Along these transects, five quadrats were placed at 1m intervals. These intervals were used to reduce bias based on ease of manoeuvrability among the kelp forests. Two steel metre-long rods were used as quadrats to facilitate operation among kelp stipes. These rods were wrapped in orange duct tape to ensure visibility while filming and were placed at right angles to create a square quadrat in which to study. Smaller quadrats of 0.25m^2 or 0.5m^2 were ruled out as mature *E. maxima* holdfasts can be large and often fuse together to cover substantial areas (Anderson et al. 1997).

Quantitative densities and estimates of relative habitat cover (%) were recorded in situ using a plastic writing slab and were transferred to paper upon finishing the dive. The percentage cover of bare rock, sand, encrusting coralline, understorey algae (species level, later grouped as foliose or turf), and drift kelp were estimated. Algae with leaf-like lamina were defined as foliose, while algae that were neither characterised as foliose nor encrusting were characterised as turf because of the vague and inconsistent definitions of what exactly a turf is (Connell et al. 2014). In this study, turf species were predominantly low-lying with small

or narrow lamina. Urchins, kelp recruits (≤150mm stipe length) and adult kelp (>150mm stipe length) of *E. maxima* were also counted. A video was taken of each quadrat to provide visual data for the results section of this thesis and to act as a back-up data source, in case writing slabs or paper datasheets were misplaced post-dive. While most data were recorded in the water, drift algae (detached algae lying on the bottom and/or attached to the urchins) were collected underwater in mesh bags and taken back to the laboratory. In a similar manner to Harrold & Reed (1985) and Blamey & Branch (2012), the wet weight (g) of drift algae was used for all analyses to ensure consistency. All algal samples were taken back to the laboratory immediately after the dive to record the shaken dry weight.

2.3 Statistical analyses

Data were analysed in R using statistical approaches and figures were created in R and Excel. Firstly, to explore the data, nested analysis of variance (ANOVA) and Kruskal-Wallis H tests were used to determine whether differences between variables were present among sites and transects nested within sites (ANOVA). To perform the parametric nested ANOVA, data had to conform to the test assumptions of normality and homoscedasticity. When these assumptions were violated, the non-parametric Kruskal-Wallis H test was used instead. In all instances data were assumed random and independent and the relevant *post-hoc* tests (Tukey and Kruskal-Wallis multiple comparisons) were used to distinguish where the inter-site differences occurred.

To further assess variability across sites, multivariate analyses were done in PERMANOVA+ for PRIMER. A Bray-Curtis measure of similarity, based on standardised data, was used to create a non-metric multidimensional scaling plot (MDS) and nested permutational analysis of variance (PERMANOVA) was then used to statistically assess differences in algal and

urchin communities between the sites (all variables combined). A canonical analysis of principle coordinates (CAP) ordination was also created to support the MDS and PERMANOVA. Furthermore, a similarity percentage (SIMPER) analysis was used to assess the within and between site similarity/dissimilarity.

To further address the research questions, all sites were analysed together and the strength and direction of correlative relationships between two variables were examined using scatterplots. Where the relationship appeared linear and no outliers were present, the parametric Pearson product-moment correlation test was used to identify whether the relationship was statistically significant, otherwise, the non-parametric Spearman rank correlation test was used instead. In both cases, this was done at the 95% confidence level. For those correlations that showed no significant relationship, variables from individual study sites were correlated to explore any site-specific patterns. A bubble plot was also created using the PLOTLY package in R, to visualise urchin density as a third dimension against kelp density and understorey algal percentage cover. To investigate differences in algal community according to *a posteriori* low (0-50) and high (>50) urchin densities derived from the correlations, another MDS plot of the data, excluding urchins, was created and PERMDISP was then used to statistically assess the spread of the data from the centroid for 'high' and 'low' densities.

3. Results

3.1 Spatial heterogeneity

Immediate underwater observations highlighted the variability within False Bay kelp forest ecosystems, even when in close proximity to one another. Urchin, kelp density and understorey algae appeared to vary considerably between sites. A-frame, for example, was the only site to exhibit 'incipient' urchin barrens (Fig. 3A). Site substrate also varied – large boulders, flat rocky shelves and sand dominated at different sites. At all sites, however, encrusting corallines covered virtually all rocky surfaces. Urchins were nearly always present on these surfaces, frequently inhabited crevices and were observed feeding on drift kelp (Fig. 3B). When surveying Buffels Bay, the diving conditions were ideal and the swell was minimal. At this site, urchins were observed climbing kelp holdfasts and stipes, both of which had visible bite marks, suggesting active feeding (Fig. 3C).

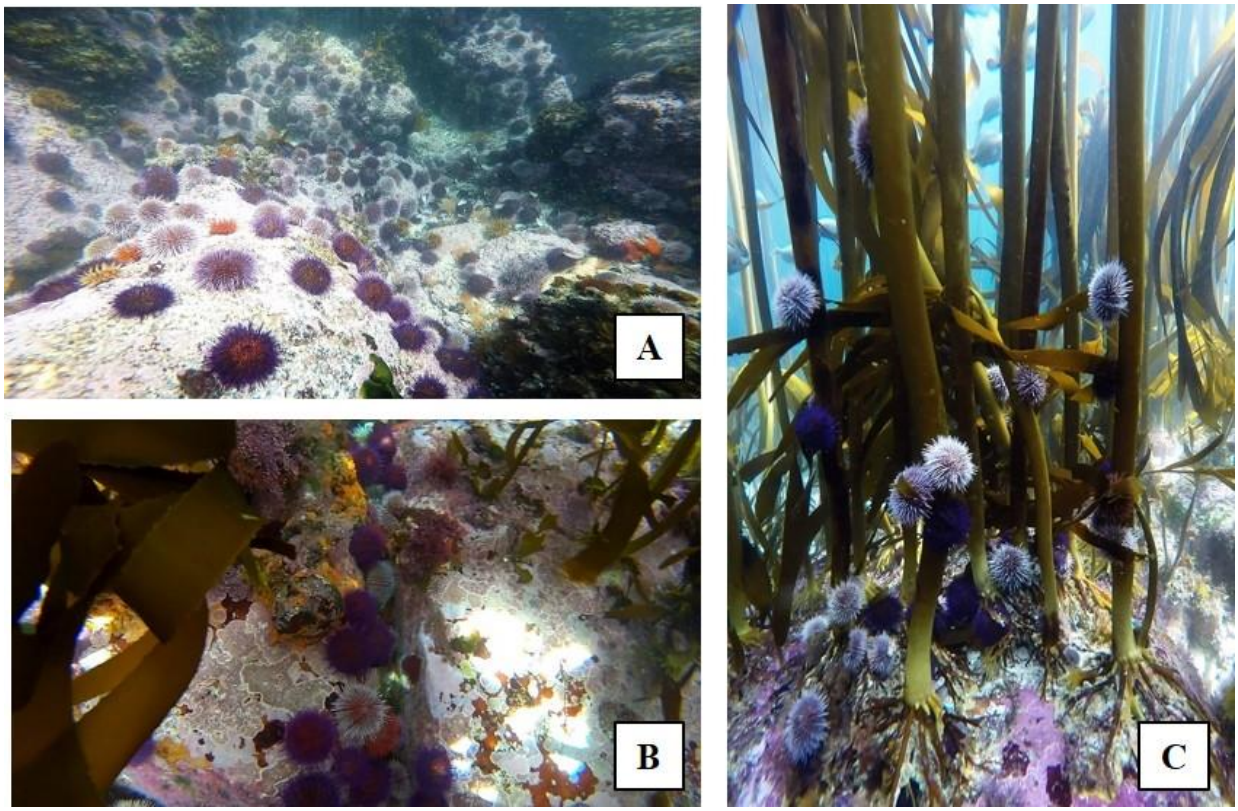
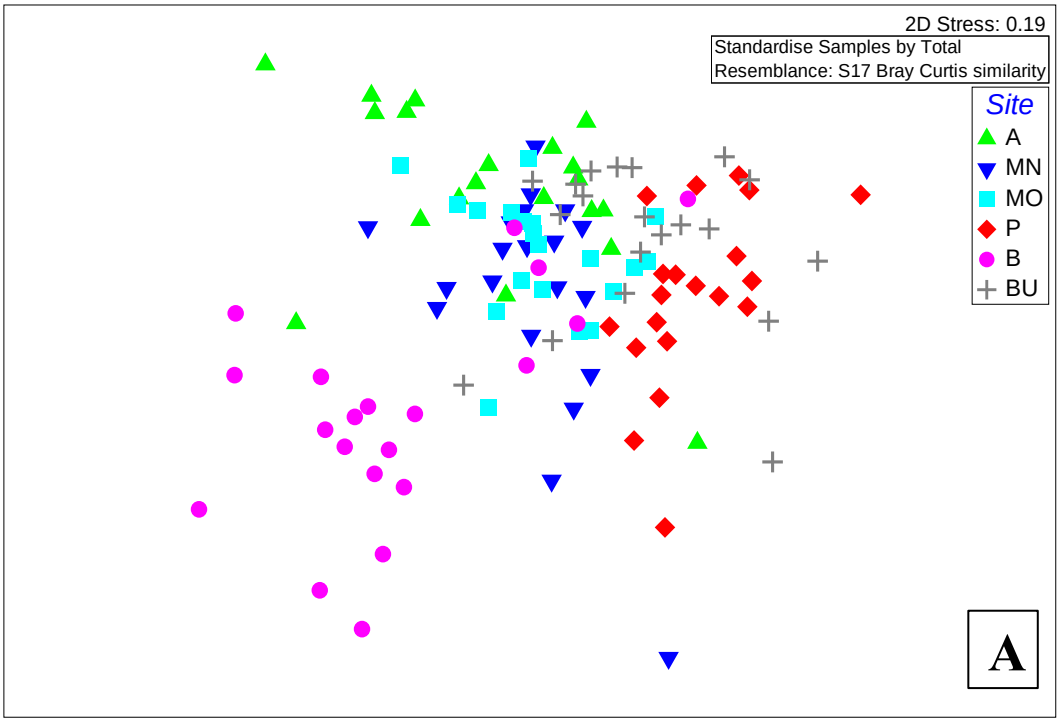


***Figure 3**: **(A)** 'Incipient' barrens observed at A-Frame, **(B)** Urchins observed inhabiting crevices at multiple sites, **(C)** Urchins observed climbing and feeding on kelp holdfasts and stipes at Buffels Bay.*

PERMANOVA confirmed that there were significant differences in urchin and algal community structure between sites (Pseudo-F = 7.91, P(perm) = 0.001) and transects nested within sites (Pseudo-F = 2.16, P(perm) = 0.001). An MDS plot allowed for visualisation of the data (Fig. 4A). Because of the fairly high-stress level of the MDS plot (0.19), a CAP ordination was used to support the MDS results (Fig. 4B). Quadrats within the same site generally experienced a certain level of similarity (ranging from 61% to 72%). However, there was a large amount of overlap between sites and variability was also present within sites (Fig. 4A & 4B). In particular, the community structure of Bordjiesrif grouped separately from the other sites (Fig. 4A & 4B), with red encrusting being most responsible for this separation (Fig. 4B). Bordjiesrif was >50% dissimilar to all other sites, yet there was also variability within this site (38% dissimilarity). Miller's Point New and Old Slipways showed the least within-site variability (33% and 28% dissimilarity respectively), and of all sites, showed the greatest similarity to each other (66% and see Fig. 4). These two sites, together with A-Frame clustered closely together, likely driven by the high abundance of urchins (Fig. 4B).



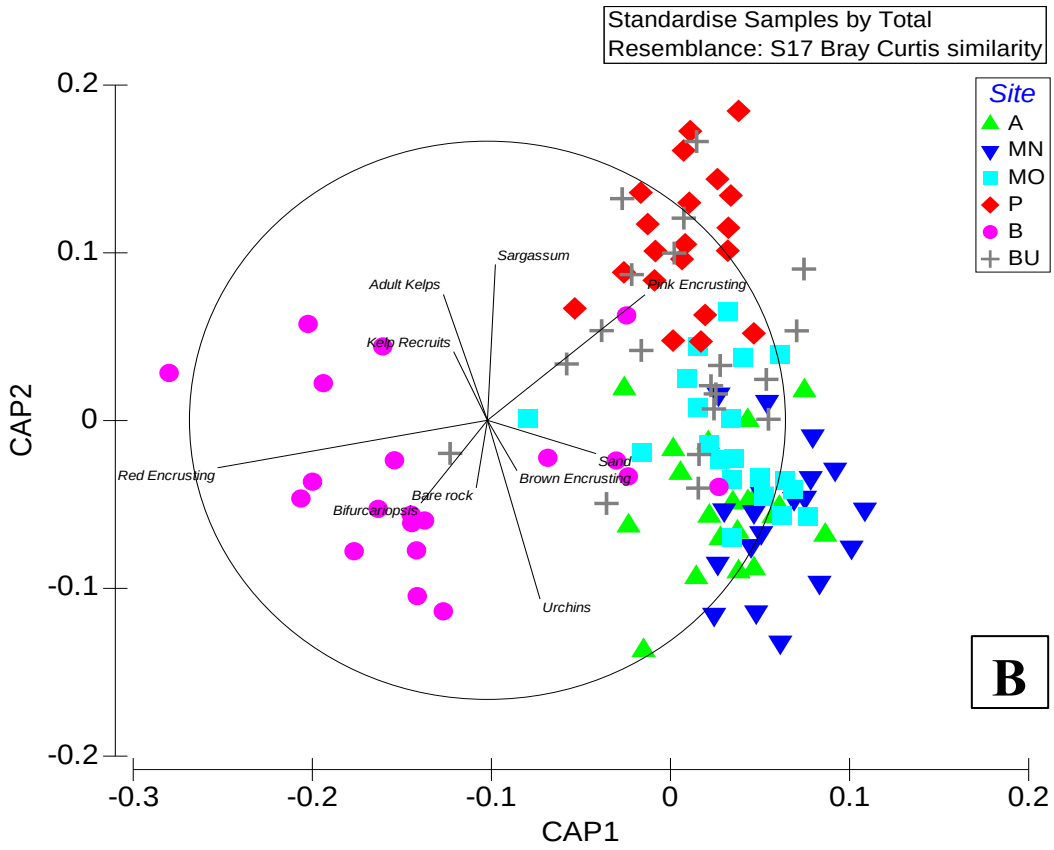


Figure 4: ***(A)*** *Multidimensional scaling plot to visualise the level of similarity across all quadrats, separated by site and* ***(B)*** *Canonical analysis of principle coordinates (CAP) ordination to identify the variables responsible for the similarity between sites. All data recorded were included in the analysis and each symbol represents a quadrat. MO = Miller's Point Old Slip, MN = Miller's Point New Slip, B = Bordjiesrif, BU = Buffels Bay, P = Partridge Point and A = A-Frame.*

Significant differences in urchin densities were found between sites ($H = 48.94$, $df = 5$, $p < 0.001$). A *post-hoc* multiple comparisons test revealed that the statistically significant differences were between Partridge Point and all other sites, except Buffels Bay, as well as between A-Frame and Buffels Bay and A-Frame and Bordjiesrif (Fig. 5A). Partridge Point had the lowest mean density of 15 urchins/m^2 and A-Frame had the highest mean urchin density of 76 urchins/m^2 (Fig. 5A). While variability was low within most sites, there was also a large upper range in urchin densities at A-Frame, with 30% of quadrats exceeding a density of 100 urchins/m^2. Miller's Point Old Slipway and Miller's Point New Slipway had mean densities of 45 and 46 urchins/m^2, respectively. Buffels Bay and Bordjiesrif were not statistically different from these means (nor themselves), and experienced mean densities of

31 and 38 urchins/m^2 respectively (Fig. 5A). In general, urchin density showed a declining trend from north to south.

Kelp densities ranged from 0-30/m^2 across all quadrats, with significant differences being most attributable to site locations ($F = 7.52$, $df_1 = 5$, $df_2 = 96$, $p < 0.001$; Table 1), whereas mean kelp density did not differ significantly between transects within ($F = 1.56$, $df_1 = 18$, $df_2 = 96$, $p = 0.086$; Table 1).

Table 1: *Results from a nested ANOVA comparing mean kelp density between sites and transects nested within sites. Df = degrees of freedom, SS = sum of squares, and MS = mean square.*

	Df	SS	MS	F	P value
Site	5	1475	294.95	7.52	<0.001
Site:Transect	18	1103	61.28	1.56	0.0862
Residuals	96	3767	39.24		

A *post-hoc* Tukey test revealed that mean densities of attached kelp at Partridge Point and Buffels Bay differed significantly from mean densities at Miller's Point Old Slipway, Miller's Point New Slipway and A-Frame, but not Bordjiesrif (Fig. 5B). Partridge Point and Buffels Bay had the two greatest mean densities of 12 and 13 kelp/m^2 respectively, whereas the other 4 sites had densities between 4 and 8 kelp/m^2 (Fig. 5B). Buffels Bay also had the largest variation, with 30% of quadrats exceeding a density of 20 kelp/m^2. In contrast to the urchins, kelp showed an increasing trend from north to south (Fig. 5B).

Abundance of kelp recruits (young sporophytes) was relatively low at all sites, with 47% of quadrats having zero recruits present. However, two quadrats (one at Partridge Point and one at A-Frame) had 20 recruits. While all sites had mean densities less than 5 recruits/m^2, a Kruskal-Wallis H test, found these small differences between sites to be statistically significant ($H = 29.82$, $df = 5$, $p < 0.001$). A *post-hoc* multiple comparisons test revealed

significant differences between Partridge Point and Buffels Bay, Miller's Point Old Slipway and Miller's Point New Slipway, as well as between Bordjiesrif and Buffels Bay, Miller's Point Old Slipway and Miller's Point New Slipway (Fig. 5C). No significant differences were found between the three sites with the lowest mean recruit density (0.5-1 recruits/m^2): Buffels Bay, Miller's Point Old Slipway and Miller's Point New Slipway (Fig. 5C). A-Frame's mean recruit density was not significantly different to any other site, but within this site there were a wide range of densities, with 20% of quadrats exceeding 5 recruits/m^2.

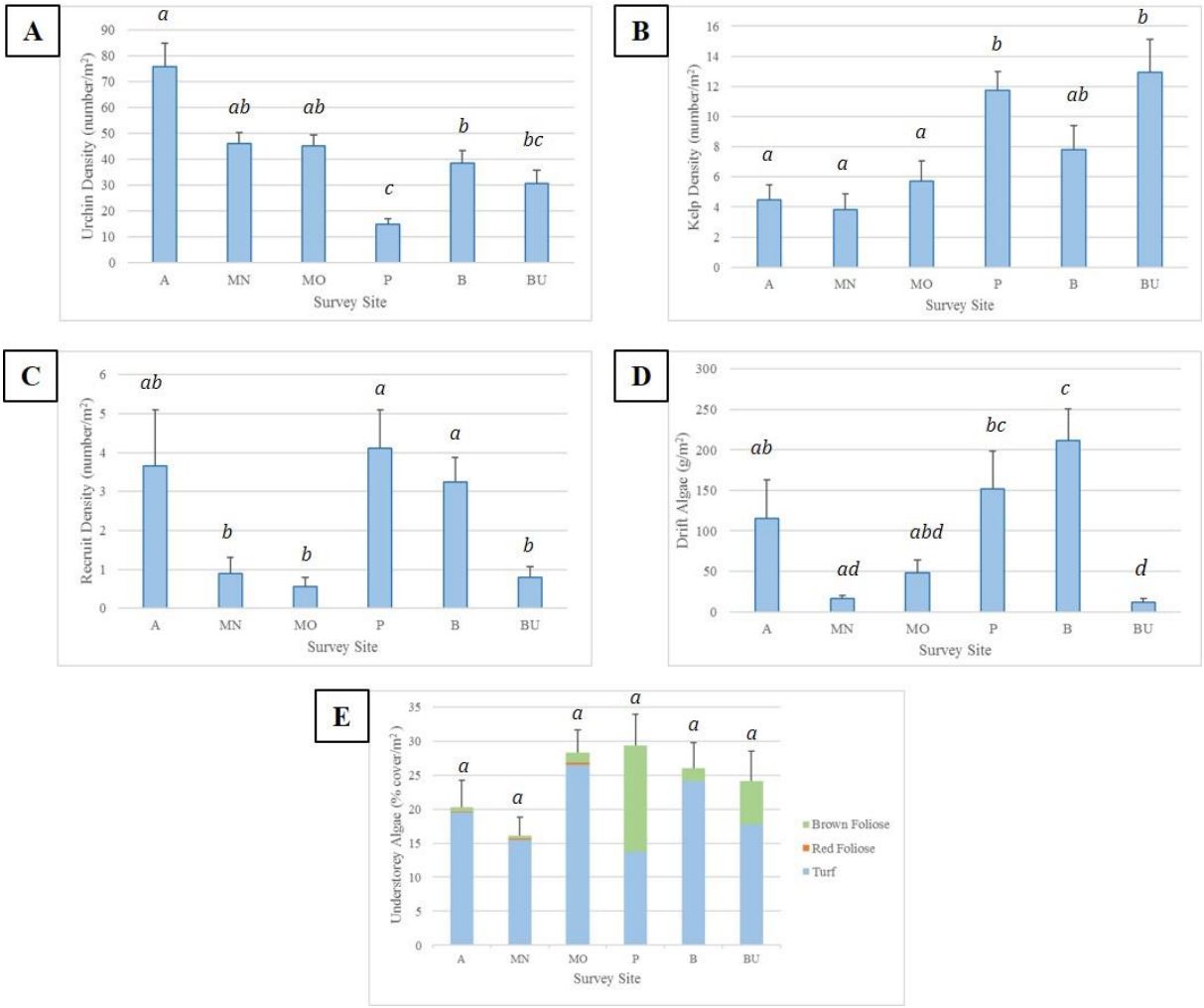


Figure 5: ***(A)*** *Mean urchin densities (number/m^2 + SE)* ***(B)*** *Mean kelp densities (number/m^2 + SE)* ***(C)*** *Mean recruit densities (number/m^2 + SE)* ***(D)*** *Mean drift algae wet weight (g/m^2 + SE)* ***(E)*** *Mean understorey algae (% cover/m^2 + SE) separated into functional groups (Brown foliose, Red foliose and Turf) for each site (A = A-Frame, MN = Miller's Point New Slipway, MO = Miller's Point Old Slipway, P = Partridge Point, B = Bordjiesrif, BU = Buffels Bay). Letters a-d above the bars determine whether the sites are significantly different (do not share the same letter) or statistically similar (share the same letter).*

Abundance of drift algae varied considerably across quadrats, with the minimum recorded wet weight being 0g/m^2 and the greatest being 893.65g/m^2. Kelp constituted >90% of all drift algae collected, with other understorey algal species (see Table 2) accounting for the remainder. 33% of quadrats had <10g/m^2 while 14% of quadrats had >200g/m^2 of drift algae, of these higher quantities, most quadrats contained sections of decaying kelp stipes. While there was some variability within sites, there appeared to be a generally increasing pattern from north to south, except for the most southern and northern sites (Fig. 5D). Differences between sites were deemed significant by the Kruskal-Wallis H test ($H = 49.02$, $df = 5$, $p < 0.001$). A *post-hoc* multiple comparisons test revealed that the sites that differed significantly were Buffels Bay and A-Frame, and Buffels Bay and Partridge Point, as well as Miller's Point New Slipway and Partridge Point. The mean drift algal quantity at Bordjiesrif was also significantly different to all other sites, except Partridge Point (Fig. 5D). There were no significant differences between the 3 sites with the lowest mean quantities of drift algae (11-49g/m^2): Buffels Bay, Miller's Point Old Slipway and Miller's Point New Slipway (Fig. 5D). Interestingly, those sites with the highest mean quantity of drift algae, also experienced the greatest variation from the mean – 30% of quadrats exceeded 200g/m^2 at both Bordjiesrif and Partridge Point, while 25% of quadrats exceeded 150g/m^2 at A-Frame.

Understorey algal cover comprised of a number of genus or species identified in Table 2, though only 'turf' and 'foliose' functional groups were examined as 'understorey algae' while encrusting species were dealt with separately. The most abundant understorey algal groups were *Codium stephansiae, Bifurcariopsis capensis, Ralfsia verrucosa and Sargassum incisifolium* with *Phaeophyta* species being most abundant overall. Partridge Point experienced the greatest quantities of understorey algae, whereas Miller's Point New Slipway experienced the least, likely a result of increased sand cover at this site (Fig. 5E). Differences

in algal quantities, however, were deemed insignificant by the Kruskal-Wallis H test ($H = 10.08$, $df = 5$, $p = 0.07$; Fig. 5E). However, significant inter-site differences were found in the foliose algal quantities ($H = 37.9$, $df = 5$, $p < 0.001$) and turf algal quantities ($H = 12.33$, $df = 5$, $p = 0.03$). Turf species dominated at all sites except Partridge Point which saw a greater quantity of brown foliose. Species characterised as red foliose were minimal at all sites (Fig. 5E). *Codium* dominated site-specific understorey algal cover at A-Frame (41% of total) and Buffels Bay (28% of total), whereas *Bifurcariopsis* dominated at Miller's Point New Slipway (39% of total) and Bordjiesrif (37% of total). At Partridge Point, *Sargassum* dominated the understorey algal cover (accounting for 53% of total), whereas *Ralfsia* dominated at Miller's Point Old Slipway (accounting for 41% of total cover).

Table 2: *Understorey algal species identified at survey sites.*

Taxonomic Group	Functional Group	Genus or Species
Rhodophyta	Encrusting Pink	*Heydrichia woelkerlingii*
Rhodophyta	Encrusting Pink	*Leptophytum foveatum*
Rhodophyta	Encrusting Pink	*Leptophytum acervatum*
Rhodophyta	Encrusting Red	*Hildenbrandia ruba*
Rhodophyta	Turf	*Champia compressa*
Rhodophyta	Turf	*Corallina officinalis*
Rhodophyta	Turf	*Rhodophylis reptans*
Rhodophyta	Red Foliose	*Plocamium sp.*
Phaeophyta	Turf	*Bifurcariopsis capensis*
Phaeophyta	Turf	*Ralfsia verrucosa*
Phaeophyta	Turf	*Zonaria subarticulata*
Phaeophyta	Turf	*Unidentified Brown*
Phaeophyta	Brown Foliose	*Anthophycus longifolius*
Phaeophyta	Brown Foliose	*Sargassum incisifolium*
Chlorophyta	Turf	*Caulerpa holmesina*
Chlorophyta	Turf	*Codium stephansiae*

Encrusting corallines were common throughout all sites, accounting for >60% of habitat cover in 79% of quadrats (data not shown). However, most of the quadrats with lower percentages of encrusting coralline cover had higher percentages of sand. Differences between sites were deemed significant by the Kruskal-Wallis H test ($H = 37.87$, $df = 5$, $p < 0.001$). Although pink encrusting corallines such as *Heydrichia woelkerlingii* and *Leptophytum foveatum* dominated 5 out of the 6 sites, small percentages of red encrusting corallines (*Hildenbrandia rubra*) were evident in 66% of the quadrats and were particularly dominant at Bordjiesrif.

The percentage cover of bare rock and sand in each quadrat was minimal (data not shown). Almost all quadrats (98%) contained less than 10% bare rock, while just 5% of quadrats contained more than 20% bare rock. These higher percentages of bare rock were found at both Miller's Point sites and Buffels Bay. The percentage cover of sand was usually below 30% (84% of quadrats) but did reach greater than 50% in 5% of the quadrats. The kelp forest at Millers Point New Slipway had the greatest cover of sand per quadrat, whereas Buffels Bay had the least.

3.2 Correlative relationships between urchins and algae

The greatest urchin density recorded during the study, was 158 urchins/m^2 (at Partridge Point), while the greatest kelp density recorded was 30 kelps/m^2 (at Buffels Bay). When these two variables were examined against one another (Fig. 6A), a weak negative association was evident, which was deemed significant ($r = -0.27$, $p < 0.01$). With the exception of three quadrats, the results suggest that above a threshold of 50 urchins/m^2, kelp density fails to increase above 10 kelps/m^2. In some instances, adult kelps were completely absent from a quadrat, even when urchin density was reduced.

Urchin density was also negatively correlated with percentage cover of understorey algae ($r = -0.28$, $p = 0.002$). Although this was not a strong negative correlation, it was deemed significant. A tenuous pattern also occurred suggesting that once urchin density reached $50/m^2$, understorey algal cover fell to below 20%. The exception was 9 quadrats, which experienced between 20-40% understorey algal cover (Fig. 6B). To explore this relationship further, urchin density was plotted against 'Foliose' and 'Turf' algae separately (data not shown). For 'Turf' algae there was no clear relationship and both the Pearson and Spearman correlation coefficient determined the relationship to be negative but statistically insignificant ($r = -0.15$, $p = 0.11$; $r = -0.01$, $p = 0.93$). Alternatively, the relationship with algae categorised as 'Foliose', was determined to be negative and statistically significant ($r = -0.24$, $p = 0.007$). A bubble plot was used to visualise the relationship between urchin density and both kelp and understorey algae (Fig. 6C). The figure shows that kelp density and understorey algal cover are generally lower when urchin density (expressed by bubble size) is greater, though there were several exceptions to this pattern.

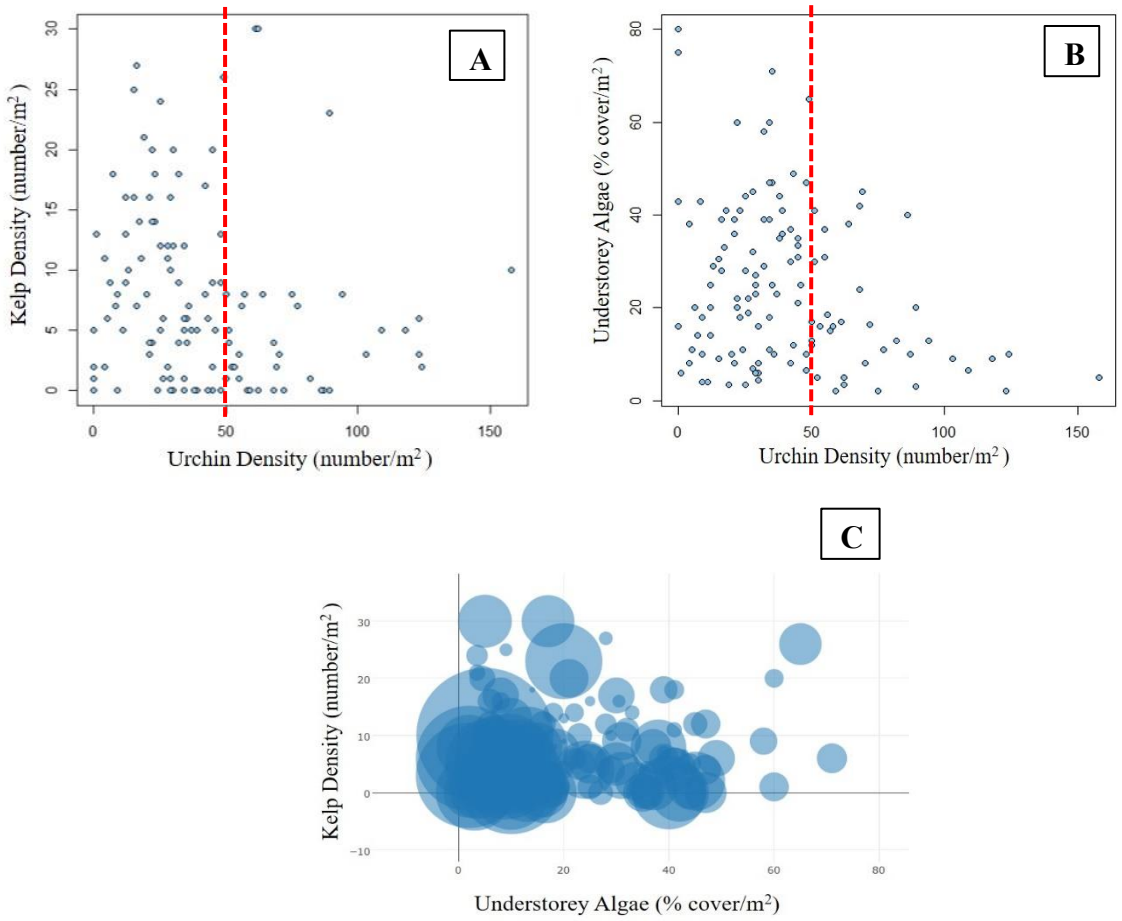


Figure 6: ***(A)*** *Scatterplot between urchin and kelp density for all sites,* ***(B)*** *Scatterplot between urchin density and percentage cover of understorey algae for all sites and* ***(C)*** *a Bubble plot of urchin density (categorised by size of bubble) plotted against kelp density and percentage cover of understorey algae for all sites.*

Algal cover was further explored using the tentative threshold of 50 urchins/m^2 determined in Figure 6A, where quadrats were *a posteriori* characterised as either having a high (>50) or low (0-50) urchin density. There was a large amount of overlap and similarity in algal cover between low and high urchin densities (Fig. 7), but a PERMANOVA found these differences to be significant (Pseudo F = 4.25, P(perm) = 0.006). The spread in the data from the group centroid between low and high urchin density quadrats was tested and no significant difference in the spread was identified (Pseudo F = 5.89, P(perm) = 0.05). However, with the exception of four quadrats, high urchin density quadrats generally clustered closer together

exhibiting similar patterns of algal community structure. The difference between community structure of high and low urchin density quadrats was greater when these four quadrats were removed from the dataset (Pseudo F = 8.36, P(perm) = 0.001), and there was now a significant difference in the spread of the data from the group centroid between high and low urchin density quadrats (Pseudo-F = 29.24, P(perm) = 0.001).

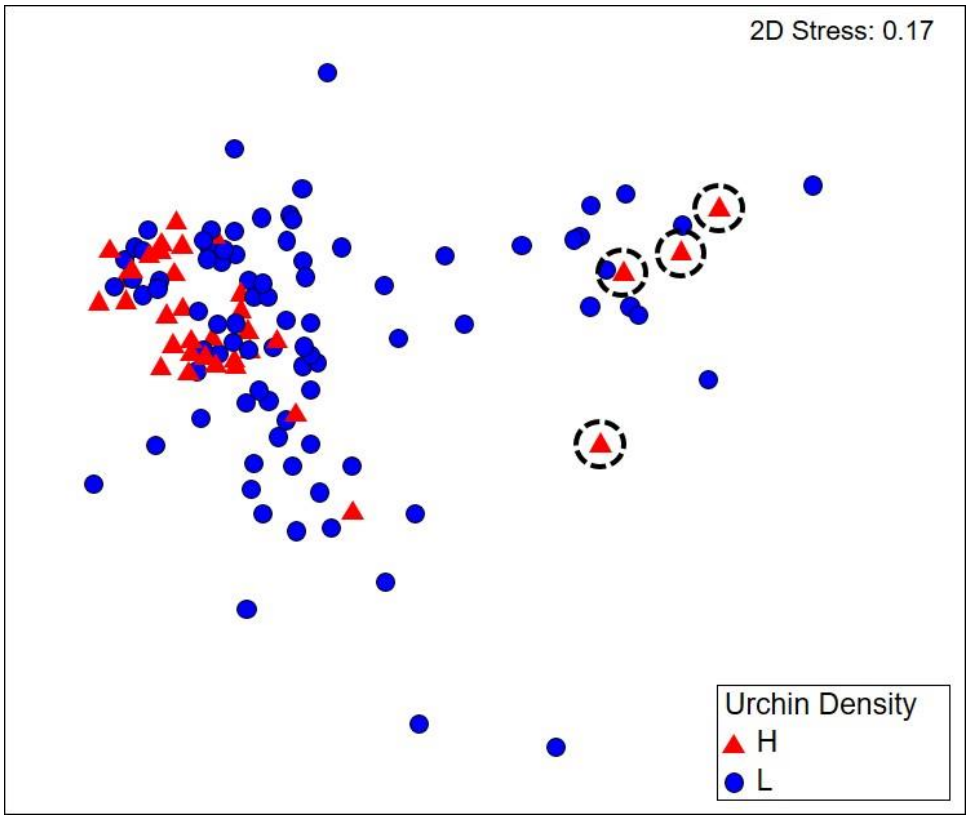


Figure 7: *Multidimensional scaling plot to visualise the level of algal similarity (sand, bare rock included) across all quadrats, grouped by high urchin density (>50) and low urchin density (0-50). PERMDISP and PERMANOVA were run with and without the four quadrats (broken circles).*

Recruit density was plotted against kelp density (Fig. 8A) and a statistically positive relationship was evident using a Spearman correlation test ($r = 0.51$, $p < 0.001$). Given that urchins can limit kelp recruitment through grazing, urchin densities were plotted against kelp recruit densities (Fig. 8B) and a Spearman correlation test determined a weak, but significant negative relationship between the two variables ($r = -0.29$, $p < 0.001$).

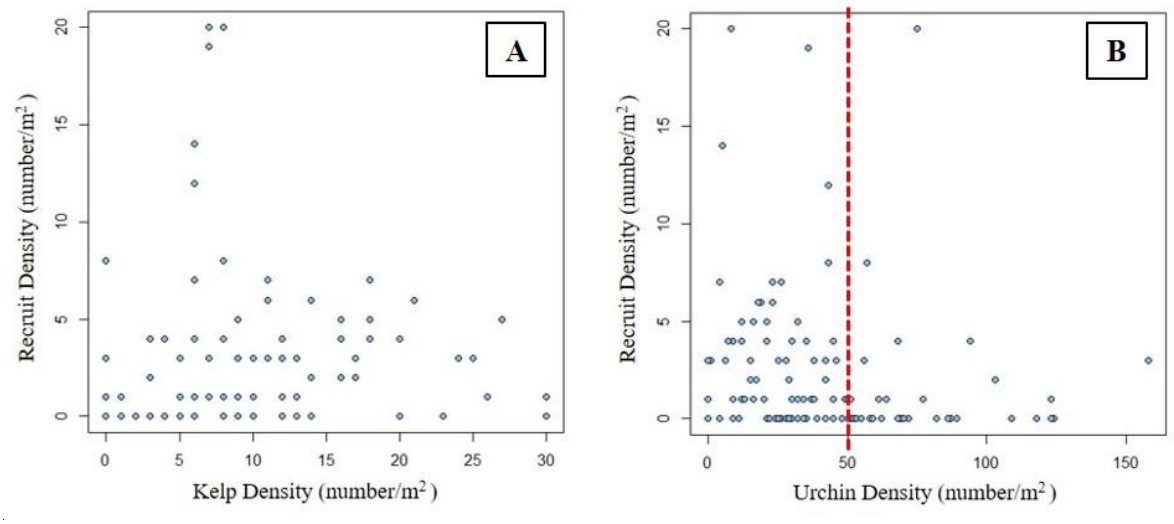


Figure 8: *Scatterplots between* ***(A)*** *adult kelps and kelp recruit density for all sites and* ***(B)*** *urchin and kelp recruit density for all sites.*

Urchin density was also plotted against the biomass of drift algae for all sites (Fig. 9A) but there was no significant relationship between the two variables ($r = 0.13$, $p = 0.14$). When individual sites were examined, the relationships were also insignificant at A-Frame, Miller's Point Old Slipway, Miller's Point New Slipway and Partridge Point (Fig. 9B-E), but a significant positive correlation was found for Bordjiesrif ($r = 0.57$, $p = 0.008$; Fig. 9F) and Buffels Bay ($r = 0.65$, $p = 0.002$; Fig. 9G).

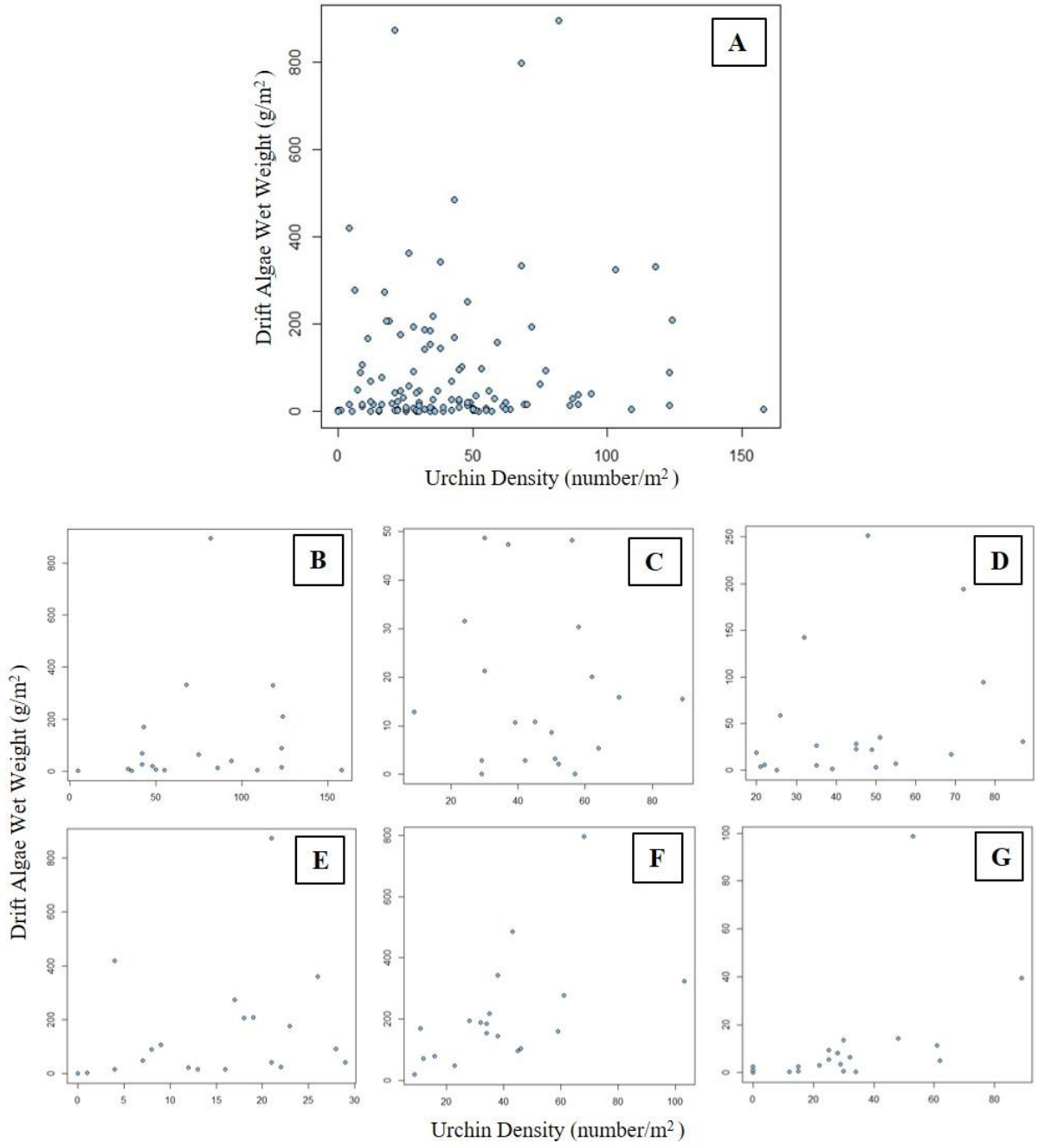


Figure 9: *Correlations between urchin density and wet weight of drift algae for* ***(A)*** *all sites combined,* ***(B)*** *A-Frame,* ***(C)*** *Miller's Point New Slipway,* ***(D)*** *Miller's Point Old Slipway* ***(E)*** *Partridge Point,* ***(F)*** *Bordjiesrif and* ***(G)*** *Buffels Bay.*

There was no significant relationship between drift algae abundance and attached kelp (r = -0.002, p = 0.97; Fig. 10A), or between drift algae abundance and understorey algae (r = -0.04, p = 0.66; Fig. 10B). When examining site-specific relationships using the Spearman correlation coefficient, there were also no significant relationships between either kelp density or understorey algal percentage and the quantity of drift algae (data not shown).

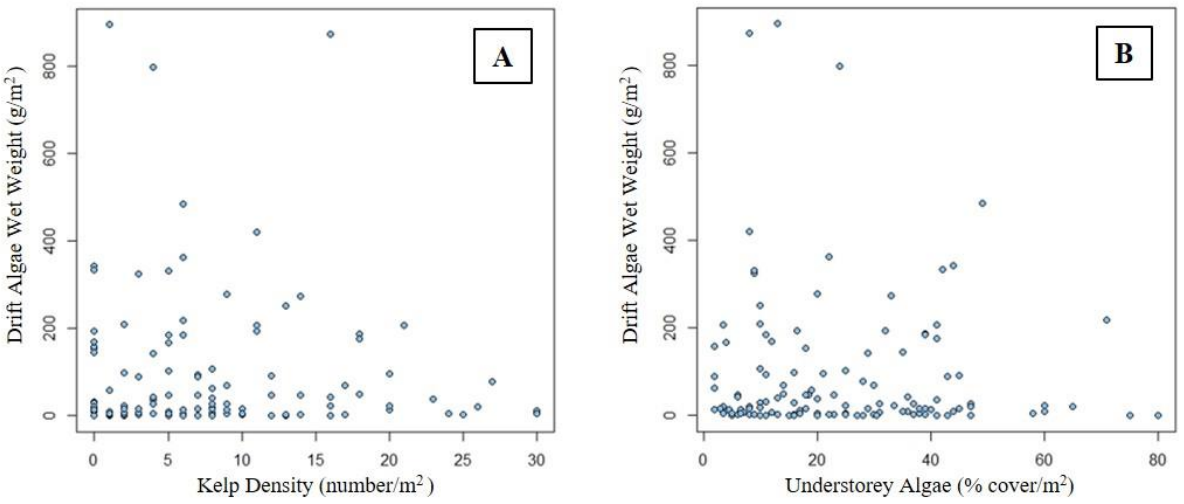


Figure 10: *Scatterplots between* ***(A)*** *kelp density and wet weight of drift algae for all sites and* ***(B)*** *% cover of understorey algae and wet weight of drift algae for all sites.*

4. Discussion

4.1 Spatial heterogeneity

Spatial heterogeneity is extremely common in subtidal habitats (Witman and Dayton, 2001). Variability in species distributions is largely attributed to physical factors such as light, temperature, sedimentation and water motion, but biological factors such as predation, competition and herbivory also play a significant role in determining spatial heterogeneity in various subtidal habitats e.g. rocky shores (Lubchenco, 1980; Valdivia et al. 2014), temperate

reefs (Andrew, 1993; Connell, 2005) and tropical reefs (Morrison, 1988; Schlacher et al. 1998). In kelp forests, physical factors such as water temperature, light penetration, substrate cover, direction of prevailing wind/current and degree of shelter, all of which vary spatially and temporally, partially determine kelp recruitment, survivorship and development (Dayton, 1985), which in turn determines understorey algal composition (Irving & Connell, 2006). For example, Reed & Foster (1984) found that dense kelp canopies can reduce bottom light to <3% of surface influx. This severe light reduction subsequently leads to declines in understorey algal cover and diversity. Additionally, the abundance and grazing pressure exerted by resident grazers plays a significant role in determining patch dynamics and algal biomass/distribution in kelp forests (Steneck et al. 2002).

In my study, all sites were within 20km of each other, situated along the western side of False Bay, a transitional zone between the cooler temperate west coast and the warmer temperate south coast (Bolton, 1986). As expected, there was a large amount of variability in urchin and algal abundance, as well as contrasting understorey algal compositions. Of the six sites, kelp densities generally increased from north to south, while urchin densities showed an opposite trend. As this study only covered the western side of False Bay, it is recommended that further research is carried out on the eastern side to see if the same directional trend is evident on the opposite side of False Bay. A directional trend in understorey algal abundance was less evident, but *Chlorophyta* and *Phaeophyta* turf and foliose species dominated significantly in the 2-5m depth range surveyed, whereas *Rhodophyta* were rare and only found in small abundances at this depth. To some extent, grazing pressure is thought to determine these algal compositions and may explain the virtual absence of red seaweeds in the False Bay shallow subtidal. For example, one experimental study found that *P. angulosus* has certain feeding preferences – it prefers the *Rhodophyta* species *Pachymenia cornea* but dislikes the

Phaeophyta species *Desmarestia firma* (Anderson & Velimirov, 1982). Algal assemblages in False Bay are evidently distinct from those west of Cape Point, where foliose *Rhodophyta* species tend to dominate in shallow (<10m) waters (Field et al. 1980; Leliaert et al. 2000), where grazers are absent. Similarly, in the area east of False Bay (Cape Hangklip – Hermanus), where urchin populations declined in the mid-1990s following an increase in predatory rock lobster, *Rhodophyta* species are now fairly abundant (L. Blamey, pers. obs.). In both of these regions, urchin densities are low, partly because they have no refuge in size from the abundant controlling predator: the west coast rock lobster *Jasus lalandii* (Tarr et al. 1996).

In False Bay kelp forests, *P. angulosus* is by far the most abundant grazer (Anderson et al. 1997). Substrate type, food availability, wave exposure and predation are all thought to play major roles in influencing the distribution and abundance of *P. angulosus* (Fricke, 1980). Leliaert et al. (2010) suggests that higher grazer densities in the shallow waters of False Bay are likely a result of lower lobster abundance and wave exposure compared to the west coast, where lobsters are known to prey on urchins and high wave intensity is thought to displace urchins to deeper, more sheltered waters (Steneck & Johnson, 2013). Others, however, argue that substrate type plays a greater role in determining abundance, and it has been well documented that urchins show a clear preference for hard substrata and occur almost exclusively on encrusting corallines (Fricke, 1979, 1980; Day & Branch, 2000). The in-situ observations of this study, confirm this finding.

Interestingly, the greatest urchin density recorded in this study, exceeded that of a previous study (90 urchins/m^2; Fricke, 1979), suggesting urchin abundance may be increasing within False Bay. This is not an unlikely scenario given that predators of urchins have been

overfished (e.g. fish; Griffiths, 2000) or have historically never been abundant in False Bay (e.g. rock lobster; Pollock and Beyers, 1981). While dense patches (up to tens of metres) of *P. angulosus* have been found on the west coast of South Africa at depths between 8 and 15m since the 1970s (Velimirov et al. 1977; Field et al. 1980), my study, found that similar 'incipient' barrens also occur in the shallow waters of False Bay. Mean urchin densities, however, show great variability. For example, Fricke's (1979) study identified a mean density of 61 urchins/m^2 at Millers Point, though a study almost two decades later recorded a much lower mean density of 6 urchins/m^2 at the same site (Anderson et al. 1997), and this study, another two decades later, recorded a mean density of 45 urchins/m^2. Site topography may influence urchin densities, however, as research suggests the distribution of certain grazers corresponds to the spatial structure of microhabitats such as crevices and rock pools (Aguilera et al. 2014). While Day & Branch (2000) found similar urchin densities on both flat and vertical surfaces, Velimirov et al. (1977) found higher urchin densities on horizontal surfaces, and this study observed higher urchin densities on vertical surfaces and in crevices (K. Morris, pers. obs.). These conflicting findings highlight the extreme variability present among kelp forests, both spatially and temporally. In some regions, the presence of 'incipient' barrens – small urchin dominated patches interspersed among intact kelp forest – is thought to be an early warning sign of large-scale kelp forest collapse (Johnson et al. 2005; Ling et al. 2015). Flukes et al. (2012) suggest that extensive urchin barrens are created through the process of patch formation, whereby the smaller barren patches gradually expand and merge into widespread barren areas. While this theory may not be applicable to all kelp forest ecosystems globally, transition zone kelp forests may be more at risk, because they are most often located towards the end of their distribution range or in regions of biogeographical overlap and are subsequently vulnerable to changes in both abiotic and biotic conditions.

4.2 Correlative relationships between urchins and algae

Kelp forest ecosystems can cope with certain degrees of stress. However, increasing anthropogenic influences and climate change implications ultimately lower the resilience of these ecosystems (Ling et al. 2009). While a gradual change in stress may have no effect on an ecosystem, once a certain stress-threshold has been exceeded, 'catastrophic shifts' may occur. If these shifts are discontinuous an alternative stable state could persist (Scheffer & Carpenter, 2003; Flukes et al. 2012). The greatest concern within subtidal ecosystems, is that urchin barrens are alternative stable states (Filbee-Dexter & Scheibling, 2014). This would mean that the tipping threshold for the forward shift to urchin barren, is greater than the recovery threshold for the reverse shift back to a kelp ecosystem. It also means that the identification of a threshold is problematic because of a likely range between the two thresholds.

My study tentatively suggests a threshold of 50 urchins/m^2 exists, above which attached kelp density fails to increase above 10/m^2, and percentage cover of understorey algae is usually limited to 20%. However, it is important to note that this threshold could be at any point within the threshold continuum and is not indicative of the complete absence of kelp. However, the negative correlations between urchin density and both kelps and understorey algae, found in this study, are broadly consistent with several other studies in the region (Fricke, 1979; Anderson et al. 1997; Blamey & Branch, 2012). The localised density threshold was transformed to biomass, using the average wet weight of *P. angulosus* for the transition zone kelp forests: 28.5g (Blamey et al. 2010). This resulted in a threshold of 1.43kg/m^2. While this threshold is specific to False Bay and cannot be generalised to other regions, it is important to critically analyse these findings in contrast to reports in the literature.

A localised urchin threshold of 1.43kg/m^2 is somewhat greater than the threshold determined by Ling et al. (2015), who collated data from 57 regime shift studies worldwide and found a mean urchin biomass (wet weight) of 668g/m^2 was the minimum biomass required for overgrazing to occur. However, without excluding studies with high urchin biomasses (>1500g/m^2), this threshold increased significantly to 2.64kg/m^2. The threshold calculated in my study is also less than the 2kg/m^2 urchin threshold for Nova Scotia, defined by Scheibling et al. (1999) and it is notably lower than the 5kg/m^2 urchin threshold for Quebec, defined by Gagnon et al. (2004). While it may be expected that cold waters in Nova Scotia and Quebec reduce urchin feeding rates, thereby increasing the biomass tipping point, research into the effects of temperature on urchin feeding rates has been inconclusive. For example, slightly increased feeding rates were observed at higher temperatures by Larson et al. (1980), but at lower temperatures by Scheibling & Anthony (2001). At first glance it, therefore, appears as though South Africa's transition zone kelp forests are more vulnerable and less resilient to grazer densities than other kelp forests worldwide. However, it is important to note that while the localised threshold does limit algal biomass to some extent, a moderate amount of kelp (10/m^2 or less) is still present above this threshold. The situation is also far more complex, as urchins exert influence over algal biomasses as a function of both their abundance (Scheibling et al. 1999; Gagnon et al. 2004) and feeding behaviour (Harrold & Reed, 1985). The small Canadian urchin *S. droebachiensis* (~50mm test diameter (TD)) for example, forms feeding fronts (aggregations of up to 500 individuals/m^2), which advance through kelp forests and destructively graze all kelps in their path (Scheibling et al. 1999; Gagnon et al. 2004). In contrast, the large Californian urchin *S. franciscanus* (up to 190mm TD), exhibits a switch in feeding mode, from largely sedentary feeding to active grazing, when there is a decline in drift kelp (Harrold & Reed, 1985).

Independent of reason, the most concerning aspect of these 'catastrophic shifts', is that kelp forest recovery may be difficult to achieve. The threshold that enables kelp recovery, ranges from 77% to 91% lower than the threshold required to initiate destructive grazing (Filbee-Dexter & Scheibling, 2014). Ling et al. (2015) estimated the biomass of urchins required to sustain an urchin dominated state as 71g/m^2, compared to the higher threshold of 668g/m^2 required to initiate a shift. This suggests that almost all urchins would need to be removed for kelp to recolonise. If this same principle was applied to False Bay, the mean urchin biomass required to sustain an urchin dominated state, devoid of most kelps, could be just 129-329g/m^2 or 5-12 urchins/m^2. This scenario does, however, assume that adult kelps would first need to decline to densities low enough for reestablishment to become difficult under dense urchin patches.

Severe kelp reductions or die-offs have been known to occur, and are often a result of extreme turbulence caused by storms. For example, an intense storm off the coast of southern California removed all canopies of giant kelp (*M. pyrifera*) from Naples Reef in 1980 (Ebeling et al. 1985). In addition, research has shown that the frequency and intensity of storms and degree of exposure influences the mortality rates of kelp forests. Frond entanglement also leads to greater kelp mortality in shallow waters (Seymour et al. 1989). Similarly, extreme thermal stress from marine heat waves has been shown to cause kelp mortality. For example, the Australian marine heat wave of 2010/11 resulted in a substantial reduction of *E. radiata,* the dominant kelp species at Jurien Bay along the Australian west coast (Wernberg et al. 2013). In light of a changing climate, an increase in the frequency and intensity of extreme events (e.g. storms and heat waves) is predicted, suggesting kelp mortalities could become more frequent (Easterling et al. 2000). Research also suggests that climate-change induced storms could lead to a decrease in kelp forest diversity and

complexity, as these ecosystems will be overwhelmed by the frequency of extreme disturbance events (Byrnes et al. 2011).

The reestablishment of kelp plants in the transitional zone may be further influenced by the self-facilitation of *E. maxima* and the feeding behaviour of *P. angulosus*. Young sporophytes are known to occur predominantly on the holdfasts of adult kelps – a form of 'nursery' providing protection from grazers (Velimirov et al. 1977; Anderson et al. 1997). These findings, however, suggest that kelp recolonisation may be increasingly difficult in the absence of attached kelp, as vulnerable recruits will have no refuge from grazers. Although *P. angulosus* is a relatively small echinoderm (60mm TD), it is thought to affect the settlement of new kelp plants by actively grazing on young *E. maxima* sporophytes (Fricke, 1979), limiting the settlement success of new kelp plants. As hypothesised, my study revealed recruit density to be inversely correlated with urchin density, suggesting there may be a causal link. In contrast to my findings and their own hypotheses, Day & Branch (2002a) found neither a positive nor negative effect on kelp recruits when urchins were experimentally removed in transition zone kelp forests. They explained these unexpected results through the presence of drift kelp and the kelp-trapping capabilities of *P. angulosus* (Day & Branch, 2002a).

Contrary to my hypothesis, however, there was no significant relationship between abundance of drift kelp and urchin density. A positive relationship was expected because urchins use their spines to trap drift algae, which they later feed on. This prevents drift algae from being swept away by the turbulent water motion of shallow subtidal environments. A higher abundance of urchins was, therefore, thought to trap a greater abundance of drift algae, thereby increasing the presence of drift algae within a quadrat. The findings of this study

were unexpected as several other studies have shown opposing results. Day & Branch (2002a) found marked reductions in drift algae at urchin removal plots, while Vanderklift & Kendrick (2005) found drift algal biomass to be four times greater in the presence of urchins (compared to absence of urchins), a result likely linked to the drift-trapping capabilities of urchins, allowing them to feed effectively. It is also widely accepted that urchins in California are sustained by drift kelp (Ebeling et el. 1985; Harrold & Reed, 1985). The most likely explanations for my unusual findings are the methodology used (collecting drift algae attached to urchins *and* floating or settled on the quadrats substrate) and the turbulent sea conditions experienced during data collection. Both sites where data were collected on days with minimal swell (Bordjiesrif and Buffels Bay), showed a positive correlation between urchin density and drift algae, suggesting localised ocean circulatory systems may be responsible for the movement of drift algae, both in and out of kelp forests.

Interestingly, urchins were observed climbing the haptera and stipes of attached kelp plants at Buffels Bay. Bite marks were clearly visible on the kelp, which supports the theory of active grazing observed by Anderson et al. (1997). This behaviour was observed during extremely calm conditions. The usually intense turbulent conditions of False Bay and the urchin's relatively small size appears to restrict the frequency of this behaviour, which may, in turn, limit the urchin's influence on macroalgal biomass. In addition, Vanderklift & Kendrick (2005) suggest that spatial subsidies in the form of drift algae from nearby kelp forests may weaken the influence of urchins on kelp forest ecosystems and the turbulent waters of South Africa could facilitate this. However, this behaviour also coincided with low drift algal abundance at Buffels Bay, suggesting that water motion may not be the only factor determining the frequency of this behaviour. My observations, therefore, imply that *P. angulosus* can switch it's feeding mode from sedentary cryptic feeding to active grazing

when drift algae are limiting; a trait also identified in its northern hemisphere counterparts *S. franciscanus* (Harrold & Reed, 1985; Ebeling et al. 1985) and *S. purpuratus* (Ebeling et al. 1985). As this behaviour was only evident at one site, it is difficult to draw definitive conclusions and further research into the feeding behaviour of *P. angulosus* in the presence/absence of drift algae needs to be addressed, preferably through controlled mesocosm experiments.

Another unexpected finding of this study was that no relationship between drift algae and kelp density or understorey algae existed. Again, I suspect this was due to localised ocean circulation moving drift algae within and outside of the kelp forests. This view is supported by Vanderklift & Kendrick (2005) who identified that drift algae collected at study sites did not match the species composition of the site, but matched the composition of a kelp forest several hundred metres away, thereby indicating the role of currents in determining drift algae distribution and abundance. Harrold & Reed (1985), however, found that composition and relative abundance of drift algae were influenced by the immediately surrounding flora. For example, high drift biomass was evident in areas with high attached algal biomass and vice versa. Studies in both the northern hemisphere (Harrold & Reed, 1985) and the southern hemisphere (Rodríguez, 2003) however, discovered important temporal variations in drift algae biomass, with drift biomass being greatest in periods of low water motion, and at a minimum during periods of high water motion. High water motion usually manifests as frequent or intense storm activity, and further studies (Ebeling et al. 1985; Dayton et al. 1992) have observed the elimination of drift algae from such events. My study was the first to explore the relationship between drift algae and attached algae in the False Bay transition zone kelp forests. Further research quantifying the biomass of drift algae during different

levels of water motion and across seasons, as well as water circulation patterns in the Bay, is, therefore, necessary to identify any possible relationships.

5. Conclusion

As expected, my findings confirm the extreme spatial variability among kelp forests and highlight the complexity of these ecosystems. Locally, this correlative research suggests that the urchin *P. angulosus* exerts a subtle influence on algal biomass and that this influence is restricted by the intense coastal turbulence of the region. For example, drift algae were found to be significantly related to urchin densities only at the two sites where data were collected in extremely calm conditions, and only under these conditions, are urchins able to feed on attached adult kelp plants.

Urchin density was inversely related to attached algae (kelp, recruits and understorey algae) and although these correlations were statistically significant, they were relatively weak in some instances. A larger sample size across False Bay, and across seasons could help to elucidate the strength of these relationships. Time and resources, however, allowed for the sample size chosen and nonetheless produced valuable indications of causal relationships, supporting the need for experimental studies on the feeding behaviour of *P. angulosus*, and the effects of its presence/absence on macroalgae, with a focus on kelp recruitment and some *Rhodophyta* species.

The structural and ecological complexity of kelp forests, as well as their economic value (e.g. Bennett et al. 2016; Blamey & Bolton *in press*), makes them one of the world's most dynamic ecosystems, worthy of further study, especially during this period of increased

stressors from climate change and anthropogenic activities (Dayton, 1985; Steneck et al. 2002; Steneck & Johnson, 2013). If climate change were to increase the intensity and frequency of storms and/or heat waves in southern Africa, resulting in increased kelp die-off, the proposed feeding behaviour of *P. angulosus* in the absence of drift algae, its suspected preference for feeding on young sporophytes, and its subsequent ability to limit algal biomass, could result in far-reaching consequences for these transition zone kelp forest ecosystems, particularly as many of them are devoid of urchin predators.

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